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ABSTRACT

THE EFFECTS OF TEMPERATURE ON THE PHYSIOLOGY OF PHATARIA UNIFASCIALIS; AND ITS IMPLICATIONS FOR THE SPECIES' DISTRIBUTION IN THE GULF OF CALIFORNIA

BY

MICHAEL BOYCE MORGAN

Populations of the asteroid Phataria unifascialis were sampled subtidally in the Gulf of California at Loreto, well within the species' distribution, and at Bahía de los Angeles (the Bay of LA), at the northern end of its distribution on several occasions between 1989 and 1991 to determine the influence of water temperature on species' physiology at each location. The starfish was much more abundant at Loreto, and though both locations had similar indices of pyloric caeca and gonad development, the population at Loreto was distinctly separated by depth into a shallow reproducing population and a deeper feeding population. No such distinct reproducing population was found at the Bay of LA. In addition, the Bay of LA population was relatively depauperate in the smaller size classes. The low winter temperatures in the Bay of LA result in reduced rates of activity and aerobic metabolism. This suggests that the lower temperatures of the Bay of LA may be in part directly responsible for the lower success there.

LOMA LINDA UNIVERSITY

GRADUATE SCHOOL

THE EFFECTS OF TEMPERATURE ON THE PHYSIOLOGY OF *PHATARIA UNIFASCIALIS*; AND ITS IMPLICATIONS FOR THE SPECIES' DISTRIBUTION IN THE GULF OF CALIFORNIA

by

Michael Boyce Morgan

A Thesis in Partial Fulfillment

of the Requirements for the Degree of

Master of Arts

in

Biology

June 1992

Each person whose signature appears below certifies that this thesis in his opinion is adequate, in scope and quality, as a thesis for the degree Master of Arts.

David L. Cowles, Chairperson
David L. Cowles, Assistant Professor of Biology

Joseph G. Galusha, Professor of Biology

Ernest R. Schwab, Associate Professor of Biology

ACKNOWLEDGEMENTS

I recognize that a project such as this would not have been possible without the expertise, guidance, and patience of my mentor, Dr. David Cowles. With deep appreciation I wish to thank him for his consistent support which proved to be a cornerstone for this project. I would also like to thank Drs. Joe Galusha and Ernest Schwab, who through their guidance and direction, helped create an atmosphere that encouraged scientific inquiry.

In addition, I would also like to thank John Reth, Bob Patton, Matt Namihas, Blake Pickering, Mark Cheneweth, Roger Lemasters, and Darla Jarrett for their respective parts in obtaining specimens.

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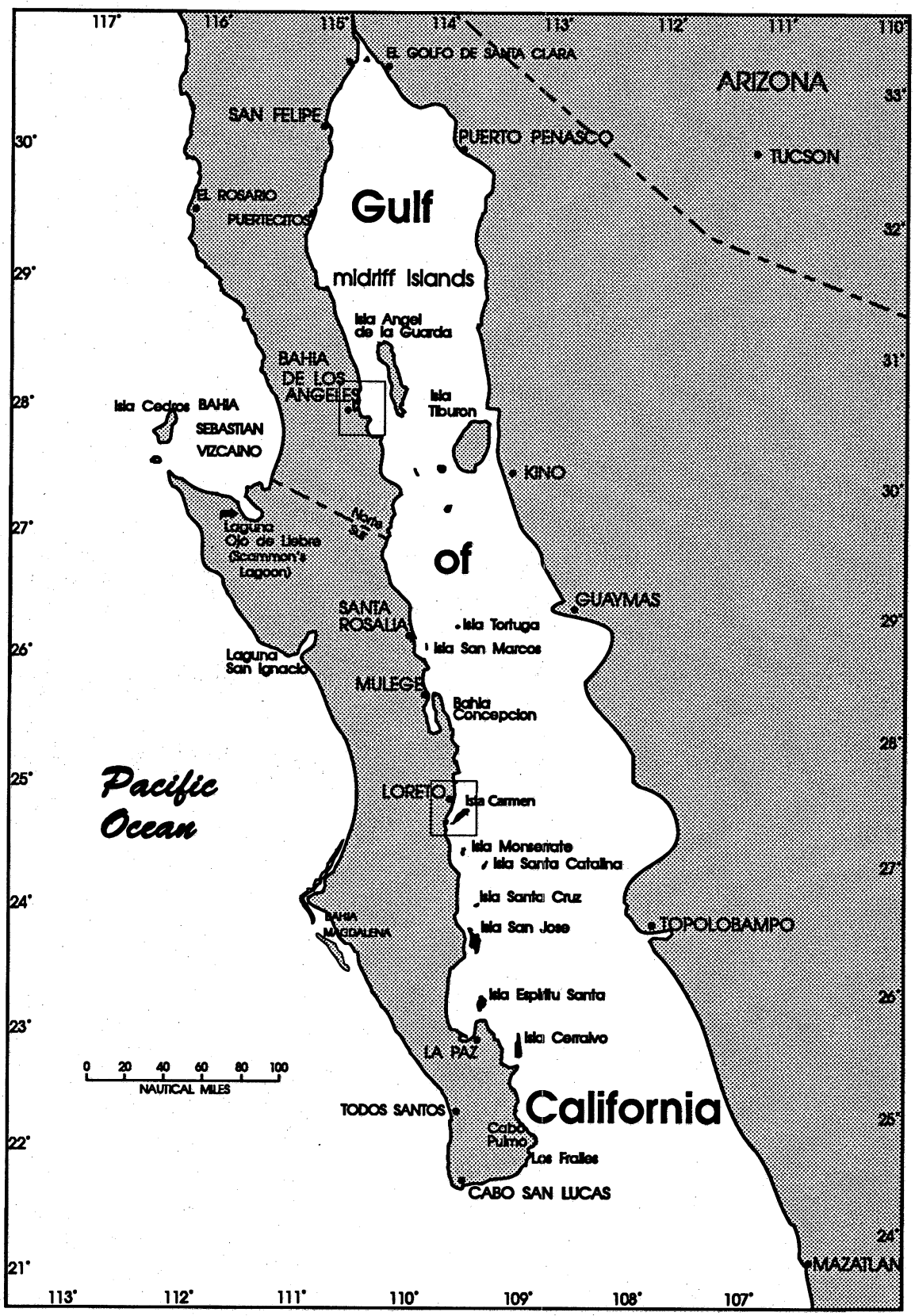
INTRODUCTION

The Gulf of California, situated between the arid land masses of the Mexico mainland and the Baja peninsula, is a unique location in which to study marine species. A comparison of the northern and southern regions of the gulf indicates there is noticeable seasonal variation in sea surface temperature, rainfall, and wind patterns due to the gulf's latitudinal range of 23° to 32°N (Figure 1). The geographic orientation of this long and narrow body of water effectively excludes major Pacific Ocean currents (Maluf 1983). In general, water circulation in the gulf exhibits surface current flow that is predominantly south-easterly in winter and spring, whereas in summer and fall, currents are less stable but appear to be northwesterly (Maluf 1983). Various regions of the gulf also have their own unique circulation patterns that are influenced by such factors as topography and bathymetry, and wind. Sea surface temperatures in the northern gulf range from 14°C to 31°C with occasional drops to as low as 10°C in the Colorado river delta area, and to as high as 32°C in some shallow tidal areas. The central and southern gulf experience generally warmer water and smaller seasonal fluctuations, from 17°C to 31°C (Robinson 1973, Hendrickson 1973). Knowledge of this environment and factors influencing it aids in understanding the distribution of gulf fauna.

Figure 1: Map of the Gulf of California and Baja Peninsula. Boxes indicate study locations. For a detailed map of the Loreto location see Fig. 3, and for the Bahía de los Angeles location see Fig. 4. (adapted from Farley and Farley 1984)


117°
116°
115°
114°
113°
112°
111°
110°
EL GOLFO DE SANTA CLARA
ARIZONA
33°
SAN FELIPE
30°
PUERTO PENASCO
TUCSON
EL ROSARIO
PUERTECITOS
Gulf
32°
29°
midriff Islands
Isla Angel de la Guarda
BAHIA DE LOS ANGELES
31°
28°
Isla Cedros
BAHIA SEBASTIAN VIZCAINO
Isla Tiburon
KINO
30°
27°
Laguna Ojo de Liebre (Scammon's Lagoon)
of
GUAYMAS
SANTA ROSALIA
Isla Tortuga
29°
26°
Isla San Marcos
Laguna San Ignacio
MULEGE
Bahia Concepcion
28°
25°
Pacific Ocean
LORETO
Isla Carmen
Isla Monserrate
Isla Santa Catalina
27°
24°
Isla Santa Cruz
BAHIA MAGDALENA
Isla San Jose
TOPOLOBAMPO
Isla Espiritu Santa
26°
23°
Isla Cerralvo
LA PAZ
0 20 40 60 80 100
NAUTICAL MILES
California
TODOS SANTOS
25°
22°
Cabo Pulmo
Los Frailes
CABO SAN LUCAS
24°
21°
MAZATLAN
113°
112°
111°
110°
109°
108°
107°

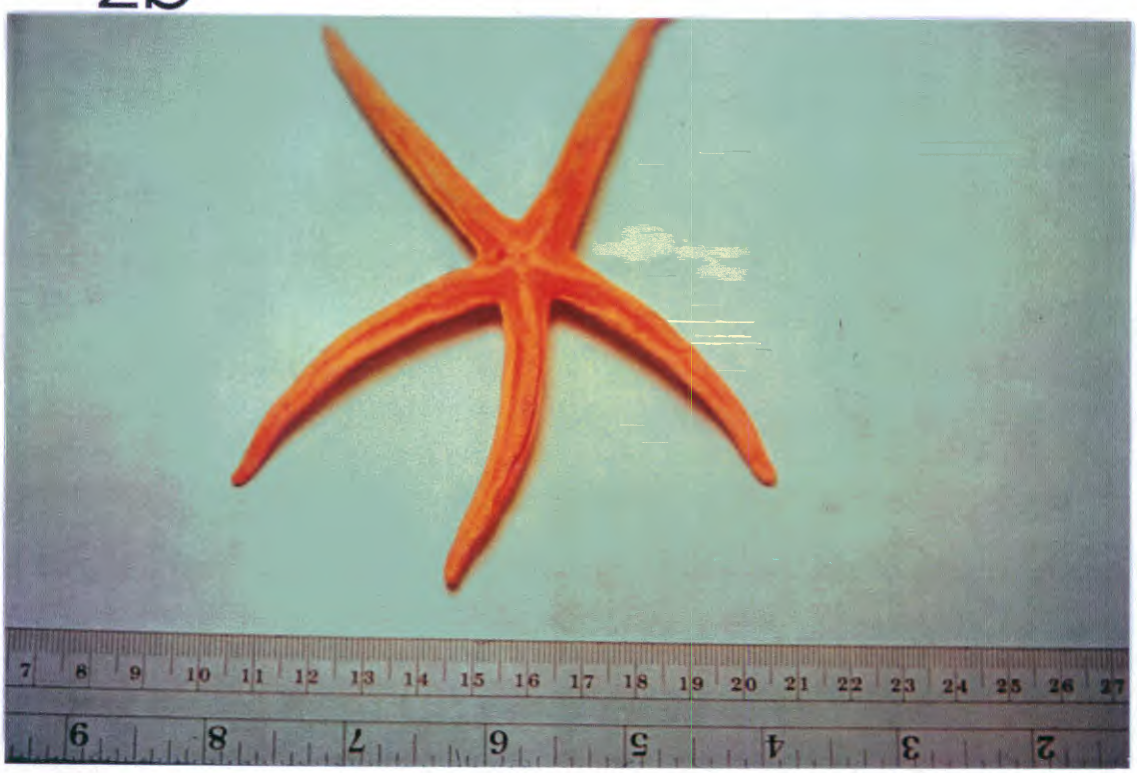
Descriptions in the literature of gulf fauna characterize species as being primarily temperate in the north, with an increasing proportion of tropical species of Panamic origin as one moves into the warmer waters farther south (Brusca 1980, Thomson, et al. 1979).

The asteroid echinoderm Phataria unifascialis Gray 1840 (Figure 2a & b) has a mostly tropical and subtropical distribution ranging from the Gulf of California to the Galapagos Islands (Maluf 1988). While this species has been reported throughout the Gulf of California, some authors report (Brusca 1980, Gottshall 1987), and my personal observations confirm, this species is much less abundant north of the midriff island region about two-thirds of the way up the gulf (see Figure 1). The large-scale distribution of some asteroids is known to be affected by water-current patterns (Birkeland 1989). Since Phataria unifascialis is found throughout the gulf, the various water currents most likely help facilitate its distribution. Therefore, some other factor(s) must be responsible for the reduced abundance observed in the northern gulf. One of the most obvious North-South differences potentially responsible for this trend is the increasingly cooler and more variable water temperature in the north. Phataria unifascialis is a shallow-water species, vertically distributed from the intertidal to depths of approximately 15 meters, so the

Figure 2: The seastar Phataria unifascialis (Asteroidea: Ophidiasteridae). Figure 2a is of live specimens. Figure 2b is of a preserved specimen.

2a

2b



cooler and more variable sea surface temperatures in the northern gulf could potentially be an important factor limiting species' abundance there. Temperature has been shown to affect feeding, digestion and absorption, and metabolic processes in echinoderms (Lawrence 1990). I therefore hypothesized that the lower temperatures found in the northern gulf might act to limit the abundance of Phataria unifascialis in this region, through measurable effects on the species' reproductive and digestive states, and/or responses in activity and respiration rates.

MATERIALS AND METHODS

Study Locations:

This study was conducted from September 1989 to January 1991 at two locations in Baja California. The first location was near the town of Loreto (latitude 25°57'N; Figure 3). The second location was Bahía de los Angeles (latitude 28°57'N, also referred to in this paper as the Bay of LA), located three degrees farther north near the midriff islands (Figure 4). Both locations were on the Baja peninsula side of the gulf. Water temperatures at the northern location (Bay of LA) ranged from 14-27°C while temperatures at the southern location (Loreto) were somewhat warmer at 17-31°C (Robinson 1973). Water temperatures of these two locations are generally characteristic of northern and southern gulf waters, respectively.

Throughout this study, a distinction was made between the terms "location" and "site". The term "location" referred to either the Bay of LA or Loreto, while the term "site" referred to a specific transect and/or collection area at one of the two locations.

The northern location (Bay of LA) was somewhat unique in that it was situated in the midriff island region of the gulf where deep water is close offshore and upwelling currents are commonly found which generally have a cooling

Figure 3: A map of the Loreto location with specific study sites: 1, Islote Chenque; 2, Juncalito; 3, Puerto Escondido North; 4, Punta Coyote; 5, Isla Danzante. (adapted from Farley and Farley 1984)

Loreto Location

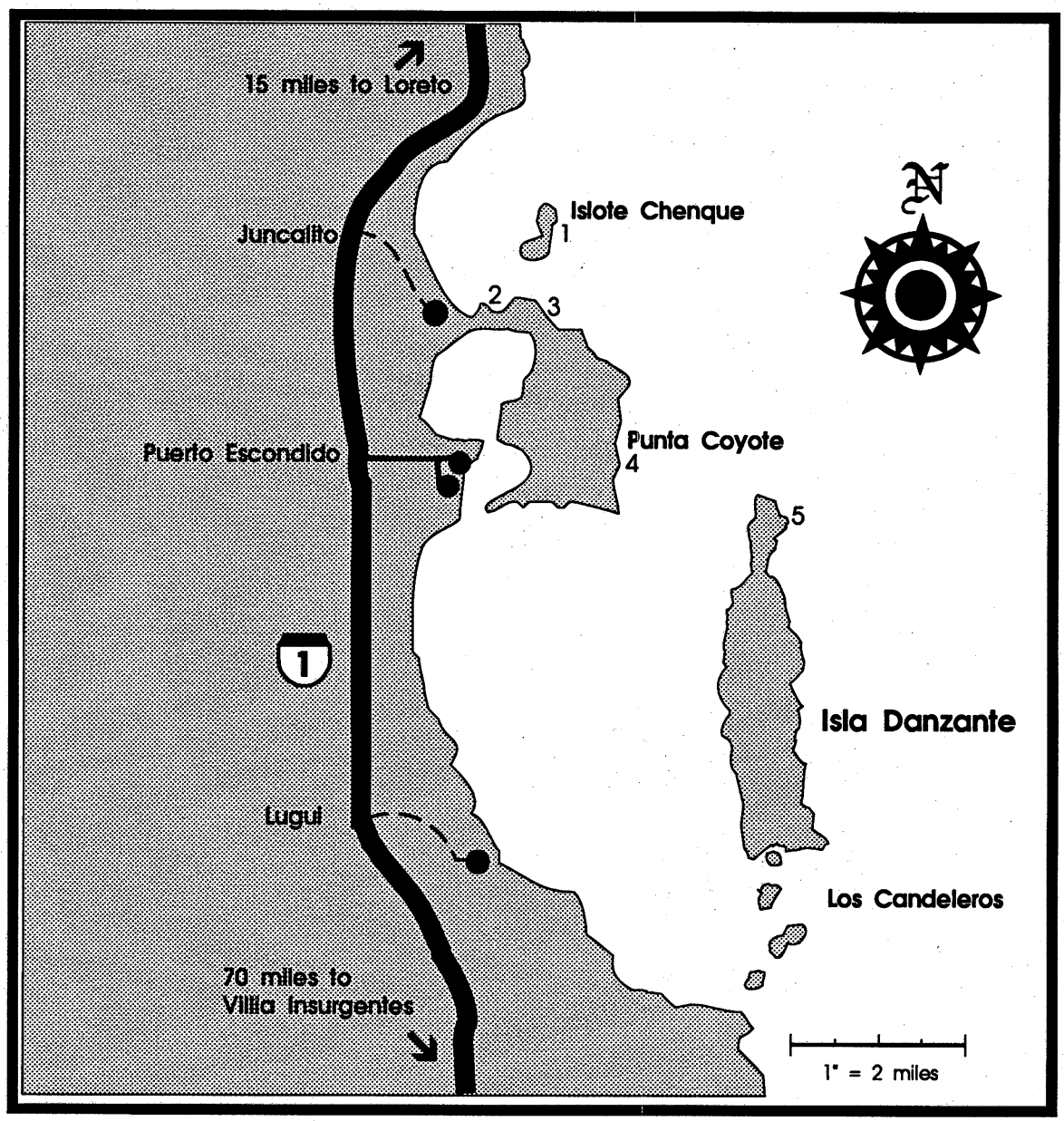
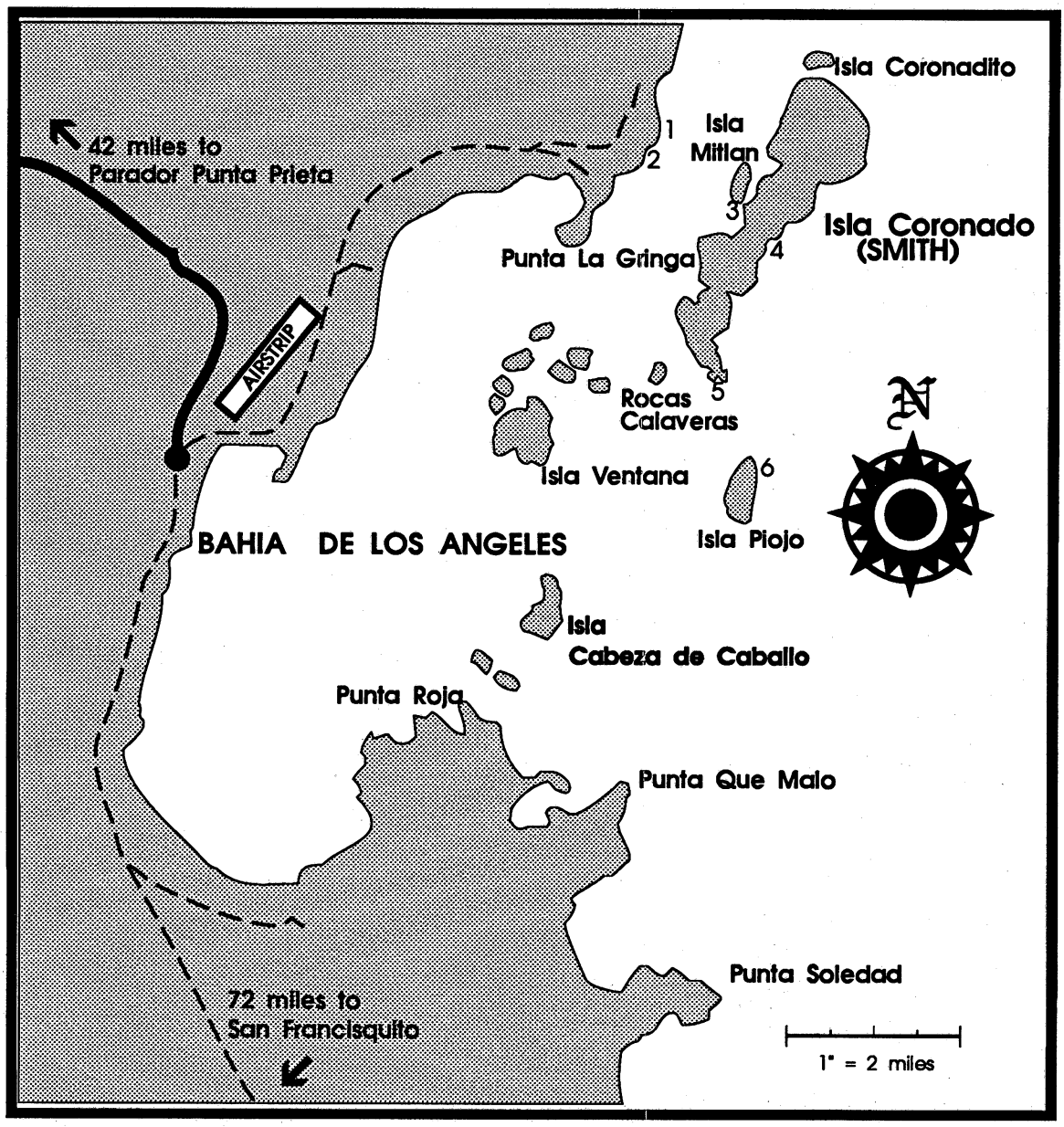


Figure 4: A map of the Bahía de los Angeles location with specific study sites: 1, Michael's Reef; 2, La Gringa; 3, Isla Mitlan; 4, Smith Island East; 5, SE Tip of Smith Island; 6, Isla Poijo.
(adapted from Farley and Farley 1984)

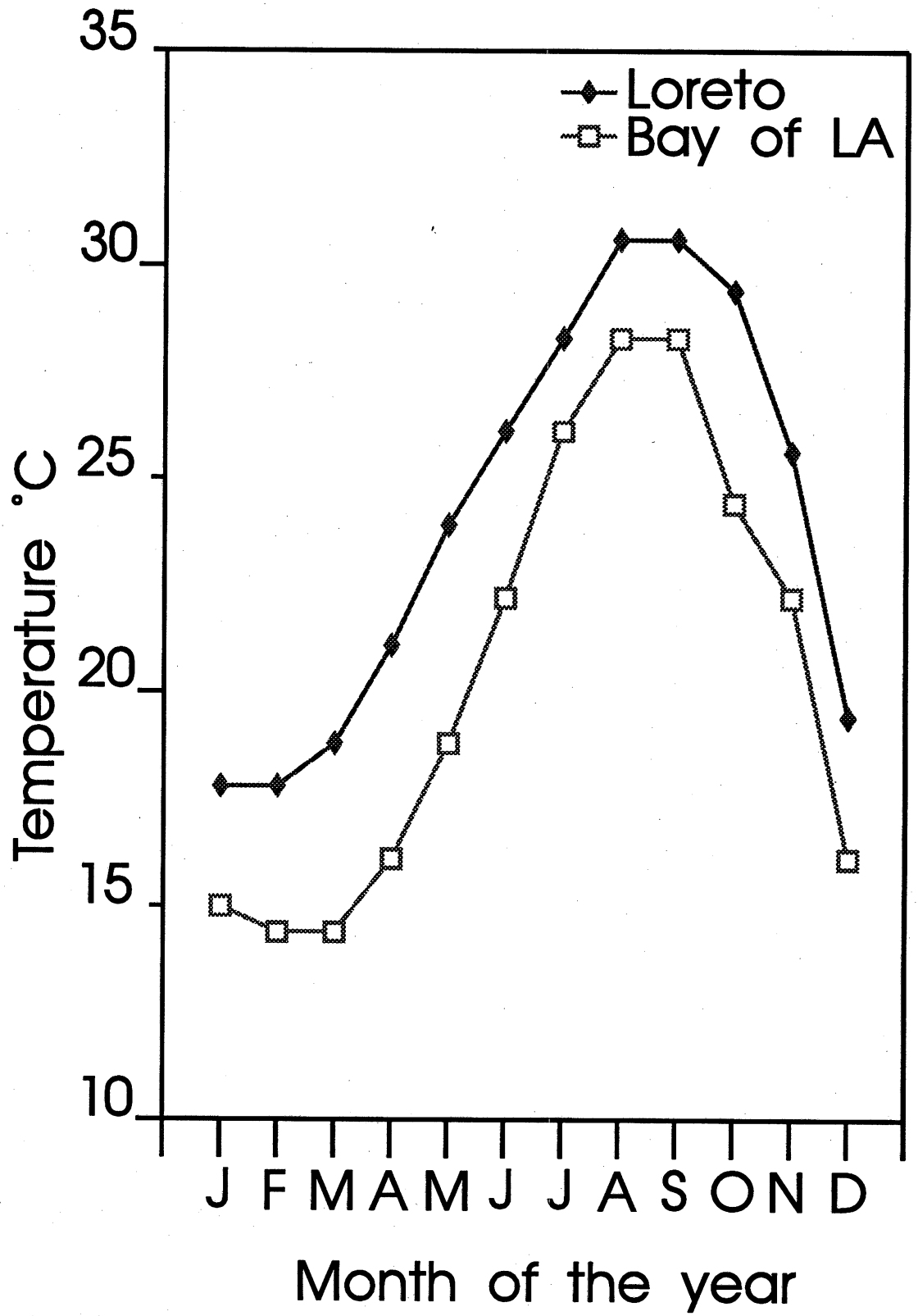
Bahía de los Angeles Location



effect on local sea surface temperatures year round (Robinson 1973, Maluf 1983). The southern location (Loreto), on the other hand, has water temperatures that stay approximately 3°C warmer than the Bay of LA year round (Figure 5).

Though Phataria unifascialis has been reported to be found on rock, boulders, coral, walls, and sand substrates (Maluf 1988), a preliminary survey indicated they were much more common on rocky areas. Specific study sites (see Figures 3 & 4) having rocky substrate and exposures to seasonal currents (Maluf 1983) were selected at each location. This species is typically a substrate film-feeder which can also feed on rock-encrusting organisms (Yamaguchi 1975, 1977, Thomassin 1976), so areas of suitable substrate consisted of rock covered with encrusting organisms such as algae and invertebrates. Areas of cobblestone were avoided due to lower amounts of biomass (Farley and Farley 1984) and the fact that on preliminary surveys I never encountered this starfish there. Although Maluf (1988) reports this species is found on sand, I found Phataria unifascialis on sand only when in close proximity to rock. For this reason, no sites were chosen on the south end of Bahía de los Angeles since substrate there was primarily sand and mud (Barnard and Grady 1968).

Figure 5: A comparison of sea surface temperatures between Loreto and the Bay of LA (Richardson 1973).


35
30
25
20
15
10
Temperature °C
Loreto
Bay of LA
J F M A M J J A S O N D
Month of the year

Population Density:

Population density of P. unifascialis was compared between the Bay of LA and Loreto in two ways. First, to determine overall population density, belt transects were randomly laid down (Overton and Davis 1969, Seber 1982) over similar suitable substrates in both locations. The belt transect was a 60 m long lead-core line marked in one meter increments. At each site, one end of the line was placed at the shoreline, and the other end extended into the water perpendicular to the shoreline. The number of P. unifascialis individuals whose central disk fell within one meter of each side of the belt were counted and tallied for each meter of the transect. Distance from the line was determined using a 1 meter long rod made from half-inch PVC pipe. The depth range of the transect was recorded for each site as well as depths at which individual specimens were found. A Chi-Square analysis was done on the species' depth distribution between both locations. Since tide charts for these locations were unavailable, all transects were done during low neap tides where the shoreline end of the transect was placed below a noticeable intertidal green band of algae.

Peak population densities were also compared between the two locations using a grid transect. Various sites were initially surveyed at each location to determine areas of

maximum population density. Then a grid made of lead-core line, covering an area of 10 meters by 12 meters, divided into one meter squares was laid out. The number of individuals that could be found within each one meter square of the grid was determined. Careful examination was made to record each starfish visible without disturbing the substrate, no rocks were turned over to find other individuals concealed underneath. Counts for each square meter were made twice and recorded on an underwater slate. The depth range over which the grid was laid was also recorded. All site transects, as well as specimen collections, were performed with the use of snorkel and/or scuba gear.

Morphological Comparisons:

At various sites within each location, specimens (≈15 to 30 per site) were randomly collected for determination of the size range of individuals. Specimens were collected from the intertidal to depths of 12 meters. This range included the majority of depths Maluf (1988) cites as this species' depth range. Shallow depth (<4.5 meters) collections were made using snorkel gear, while greater depths (>4.5 meters) required scuba gear. For size measurements, animals were weighed to the nearest 0.001g on a table top balance, and ray length was recorded to the

nearest 0.1 cm. The ray length was determined by measuring the distance from the mouth to the tip of the longest ray. A t-test (Sokal and Rohlf, 1973) was used to compare differences in size between shallow living versus deep living starfish at each location, as well as possible size differences between the two locations.

While collecting specimens for size measurements, records were also taken to determine the number of individuals found eating. As an individual was picked up, it was immediately turned over to see if its stomach was everted. All individuals with everted stomachs were recorded as eating. A test of significance of the difference between two proportions was performed on the proportion of individuals eating versus not eating (Kuzma 1984).

Assessment of in situ physiological and reproductive states:

A determination of P. unifascialis' pyloric cecal and gonadal development was made in the spring of 1990 at each location. Specimens were collected and grouped by depth using procedures already described. Initially a specimen was weighed and the longest ray length measured. One ray was then removed at its base from the central disk and reweighed before beginning the dissection. During the dissection, the ray was cut in half dorsoventrally using the

ambulacral groove as a guide. With the ray in two halves, the pyloric caecum was removed and the ray reweighed. Next the gonad tissue was removed and the ray again reweighed. Weights of pyloric caecum and gonads were calculated as differences between arm weight before and after their removal. In addition, a subjective visual classification of gonad tissue was made prior to its removal. For this classification, gonad size was characterized as none visible, extra-small, small, medium, large, and extra-large. A Chi-square test (Kuzma, 1984) was performed on this evaluation to test for homogeneity.

Activity Rates:

Activity rates were obtained by turning a specimen over and recording the time (in seconds) required to right itself (Stickle and Diehl 1987). These values were then divided by 1000 to obtain an activity coefficient. For this test, specimens (≈30) from both locations were subjected to temperatures of 13, 14.4, 17.8, 22, 25, 27, and 31°C. These temperatures represent the entire range encountered by the species in the gulf plus one temperature (13°C) slightly cooler than normal.

Specimens from Loreto were tested in the laboratory during February 1990 after they had acclimatized in an aquarium system with natural seawater at 24°C ±1° for one

month. The aquarium system had been inoculated with seawater from the gulf. Loreto specimens were fed red and green algae introduced on rock taken from the Pacific ocean as well as algae that was cultured in the aquarium system.

Specimens from Bahía de los Angeles were tested on location during January 1991 using a 15 gallon aquarium connected to a recirculating heating and cooling water bath. The ambient water temperature in Bahía de los Angeles at the time of this experiment was 16°C. An Analysis of Variance and Scheffe's test (Norusis 1990) were done to compare activity coefficients between locations and between temperatures.

Temperature Effects on Rates of Oxygen Consumption:

Rates of oxygen consumption for P. unifascialis at different temperatures were measured in the laboratory. For this analysis, 6-12 specimens were used at each temperature. Each specimen was placed in an enclosed respiration chamber. Temperature within each chamber was controlled and maintained by a water jacket. Chambers used were 200 ml or 2000 ml, depending on specimen size. Bacterial growth and respiration in the chambers were retarded by exposing the chamber water to light from an ultraviolet sterilizer for 10 minutes, as well as the addition of 25 mg/l of streptomycin and penicillin to the water. Rate of oxygen consumption was

measured using of Clark-type oxygen sensing electrodes (Clark, 1956) connected to an amplifier. Analog signals from the amplifier were converted to digital form with the use of a Data Translation DT-2805 A-D board connected to an IBM personal computer. The time-dependent change in oxygen level was recorded and analyzed using custom software programs PROBES and ANALYZE (Cowles 1987). All final measurements were expressed in units of μmol O_2/(g wet wt x h).

RESULTS

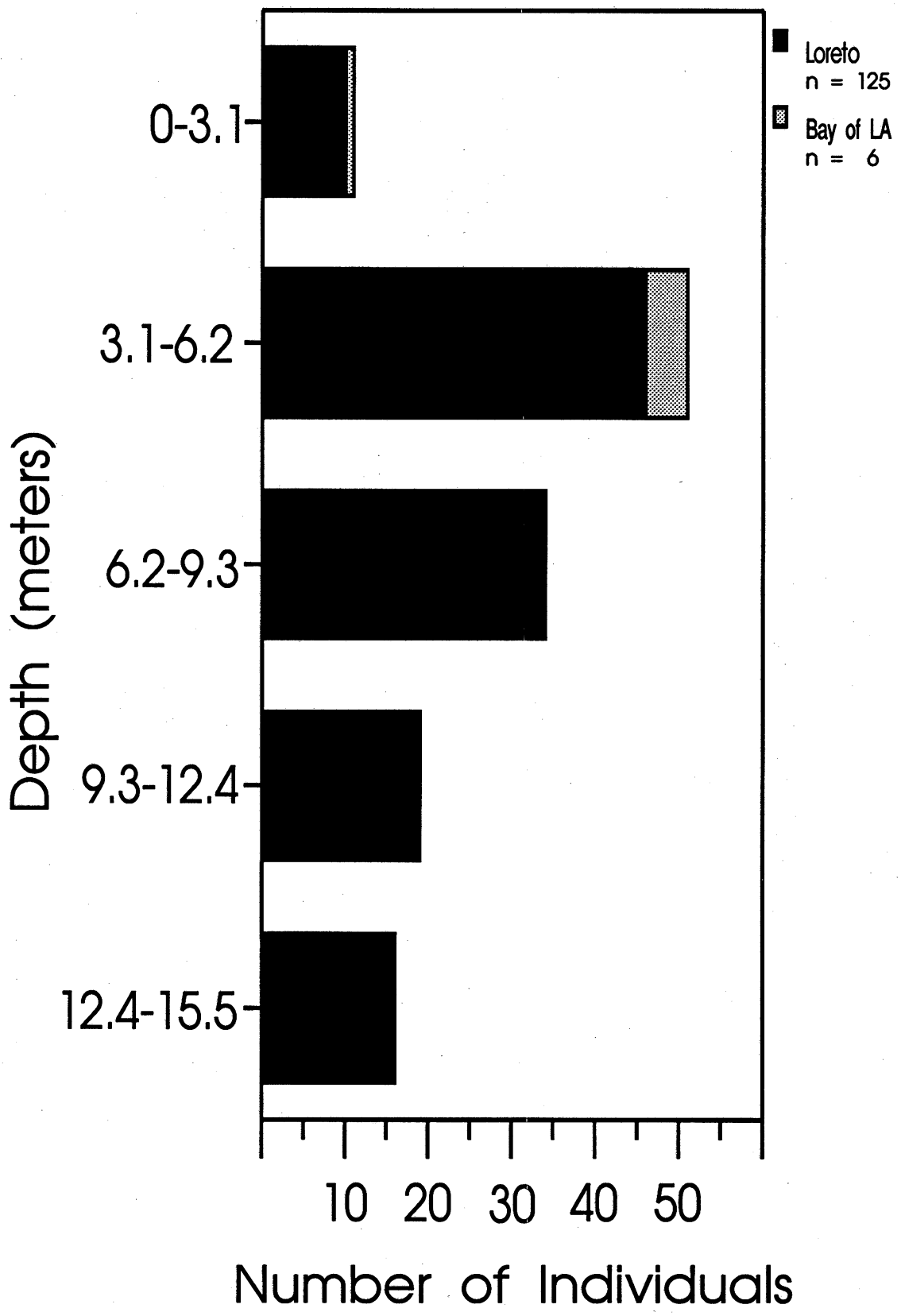
Population Density:

Loreto's population density ($\bar{x}$ = 30.5 individuals/120m^2, sd=27.98, n=4) was greater than the density at the Bay of LA ($\bar{x}$ = 1.2 individuals/120m^2, sd=2.17, n=5). At the Bay of LA, some of the belt transects had zero specimens, so prior to a comparative analysis of the two locations, the data were manipulated by adding .5 to each measurement and then taking the square root. All measurements from both locations were manipulated in this manner (Sokal and Rolhf, 1973). A t-test of transformed data indicates that the Loreto sample is significantly greater ($t=2.39$, $df=7$, $p<.05$) than the sample from the Bay of LA.

Depth Distribution:

Individuals were most frequently encountered between the depths of 3.1 and 6.2 meters (Figure 6). These data were collected at the time of the belt transects. Depth distributions between Loreto and the Bay of LA were similar ($\chi^2=7.03$, $p>.05$, $df=4$).

Figure 6: Depth distribution results from belt transects. Data from both Loreto and the Bay of LA are shown.


Loreto
n = 125
Bay of LA
n = 6
0-3.1
3.1-6.2
6.2-9.3
9.3-12.4
12.4-15.5
Depth (meters)
10 20 30 40 50
Number of Individuals

Peak Abundance:

A difference existed in peak population densities between the Bay of LA and Loreto. At the Bay of LA an average of only 5 specimens/120m^2, (n = 2, sd = 1.41) were found in the most dense aggregations, whereas at Loreto densities averaged 66 specimens/120m^2, (n = 3, sd = 37.4).

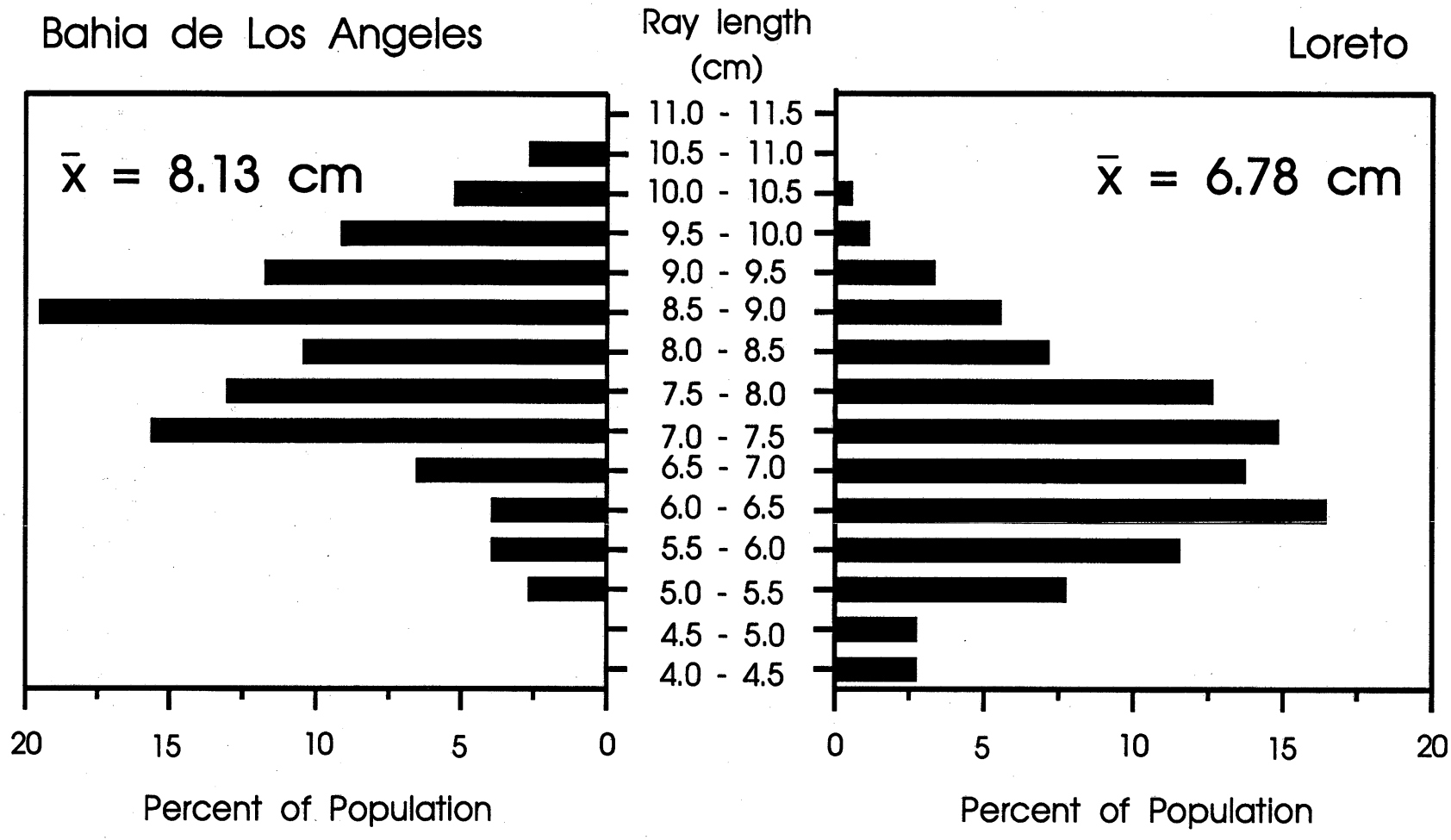
Size comparisons between the Loreto and Bay of LA:

A total of 320 animals were used to compare body sizes between the two locations, 213 from Loreto and 107 from the Bay of LA. A summary is shown in Table 1. Averages from the southern location (Loreto) were consistently and significantly ($p<.05$) smaller than those of the northern location (Bay of LA) in all categories described. The mean total wet weight of individuals from the Loreto population ($\bar{x}$ =23.54g) was significantly smaller ($p<.05$) than the weight of Bay of LA individuals ($\bar{x}$ = 34.43g). A comparison of ray lengths (Figure 7) indicates the Loreto population ($\bar{x}$ = 6.78cm) had significantly shorter rays ($p<.05$) than the Bay of LA population ($\bar{x}$ = 8.13cm).

Table 1: A comparison of several measures of the average size of individuals between Loreto and the Bay of LA. Student t-scores and probability values are for comparisons between the populations at the two sites.

	Loreto			Bay of LA			t-score	probability
	mean	sd	n	mean	sd	n		
Total wet weight (g)	23.59	9.94	30	34.43	9.68	30	4.27	p<.0001
Ray length (cm)	6.78	1.21	184	8.13	1.33	77	7.99	p<.0001
Ray weight (g)	3.87	1.64	30	5.75	1.57	30	4.53	p<.0001
Pyloric Caeca weight (g)	.90	.47	30	1.30	.39	30	3.71	p<.0001
Gonad weight (g)	.167	.13	30	.297	.19	30	3.08	p<.0001

Figure 7: A comparison of ray length distributions between Loreto (n=184) and Bay of LA (n=77).


Bahia de Los Angeles
Ray length
(cm)
Loreto
x̄ = 8.13 cm
x̄ = 6.78 cm
11.0 - 11.5
10.5 - 11.0
10.0 - 10.5
9.5 - 10.0
9.0 - 9.5
8.5 - 9.0
8.0 - 8.5
7.5 - 8.0
7.0 - 7.5
6.5 - 7.0
6.0 - 6.5
5.5 - 6.0
5.0 - 5.5
4.5 - 5.0
4.0 - 4.5
20
15
10
5
0
0
5
10
15
20
Percent of Population
Percent of Population

The average ray weight at Loreto ($\bar{x}$ = 3.87g) was significantly less ($p<.05$) than the ray weight of the Bay of LA ($\bar{x}$ = 5.75g). The amount of pyloric caeca found at Loreto ($\bar{x}$ = 0.90g) differed significantly ($p<.05$) from the amount found at the Bay of LA ($\bar{x}$ = 1.3g). Comparison of gonad weight indicates Loreto populations ($\bar{x}$ = 0.167g) were significantly less ($p<.05$) than the Bay of LA population ($\bar{x}$ = 0.297g). A visual classification of gonads, however, indicates that at Loreto the amount of gonads visible was similar to the amount visible at the Bay of LA.

Comparisons of shallow and deep at each Location:

Comparisons of shallow and deep populations at Loreto indicate the deep population was significantly smaller ($p<.001$) in all categories of size measurements. In contrast, at the Bay of LA there was no significant difference between shallow and deep for all categories of size measurements (Table 2).

Regression Analysis:

A regression analysis was done by comparing variable pairs from both locations. The relationship of Pyloric Caeca Weight/Total Wet Weight indicates that there was a significant difference (ANCOVA, $p<.05$) in the slopes of this

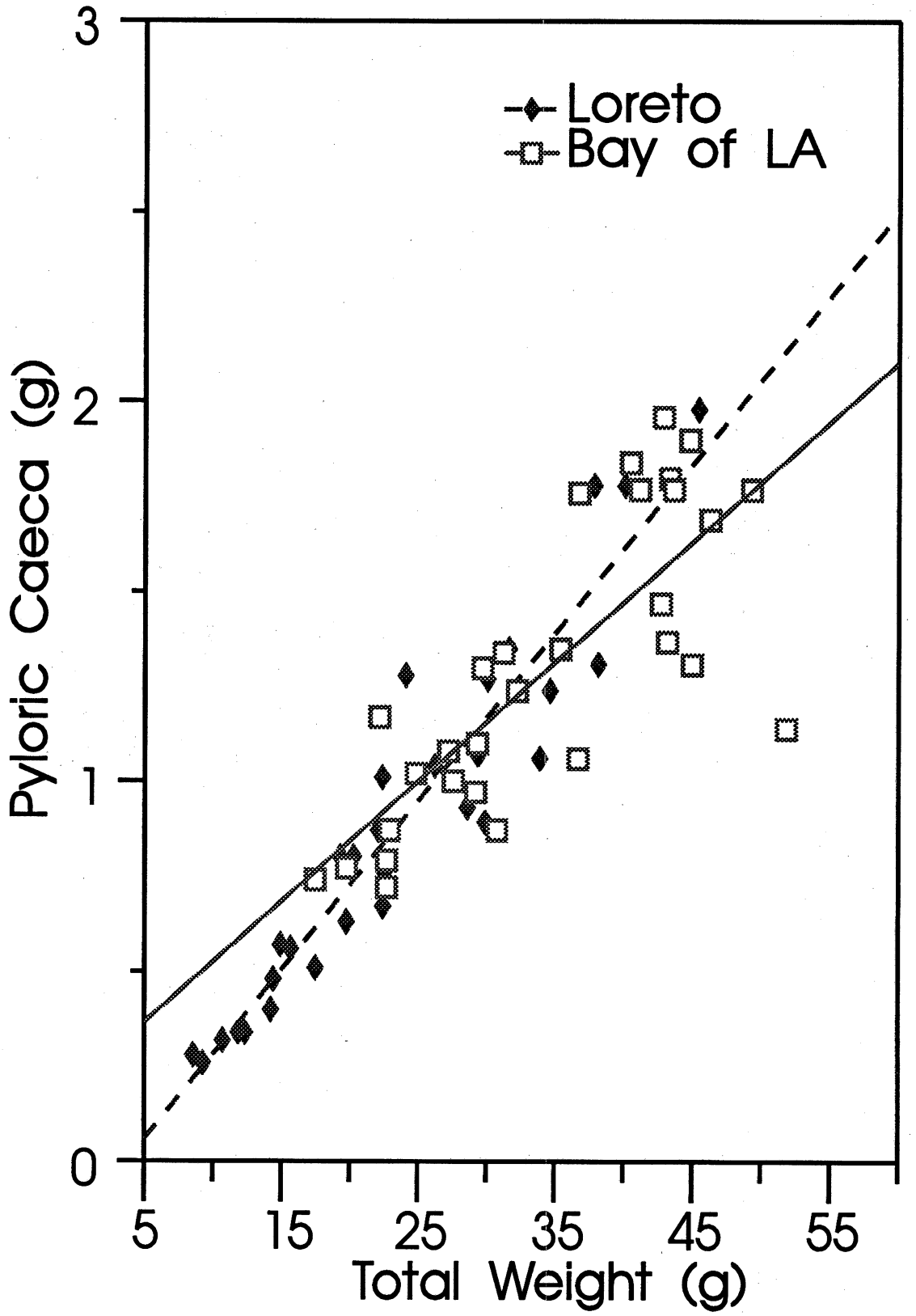
Table 2: A comparison of several measures of body size between shallow (<4.5 meters) and deep (>4.5 meters) living individuals at Loreto (2a) and the Bay of LA (2b). Student t-scores and probability values are for comparisons between shallow and deep individuals.

2a-**Loreto**	Shallow			Deep			t-score	probability
	mean	sd	n	mean	sd	n		
Total wet weight (g)	31.18	7.42	15	16.01	5.13	15	6.51	p<.0001
Ray length (cm)	7.45	1.12	92	6.09	.88	91	9.13	p<.0001
Ray weight (g)	5.16	1.15	15	2.62	.96	15	6.47	p<.0001
Pyloric Caeca weight (g)	1.26	.36	15	.54	.23	15	5.66	p<.0001
Gonad weight (g)	.255	.11	15	.078	.0066	15	5.40	p<.0001

2b-**Bay of LA**	Shallow			Deep			t-score	probability
	mean	sd	n	mean	sd	n		
Total wet weight (g)	33.22	11.72	15	35.64	7.32	15	.678	p>.95
Ray length (cm)	7.95	1.29	33	8.27	1.36	44	1.02	p>.95
Ray weight (g)	5.61	1.87	15	5.89	1.27	15	.47	p>.95
Pyloric Caeca weight (g)	1.27	.42	15	1.33	.34	15	.218	p>.95
Gonad weight (g)	.312	.24	15	.282	.15	15	.439	p>.95

relationship between the two locations (Figure 8). At the Bay of LA, smaller specimens had a greater proportion of pyloric caeca ($\hat{y} = 3.159x10^{-2} x + 0.21009$, $n = 30$, $r^2 = .61$), whereas the larger specimens with the greatest amounts of pyloric caeca were found at Loreto ($\hat{y} = 4.437x10^{-2} x + -0.1610$, $n = 30$, $r^2 = .90$,). This regression (see Figure 8) is also representative of the trend found with other variable pairs. The ratio of Ray Length/Total Wet Weight for Loreto was also significantly different from the ratio at the Bay of LA (ANCOVA, $p<.05$). Small specimens with longer ray lengths were found at the Bay of LA ($\hat{y} = 0.1046 x + 5.5437$, $n = 30$, $r^2 = .87$), but this trend did not continue into the larger size classes where the larger Loreto specimens had longer ray lengths ($\hat{y} = 0.1276 x + 4.8029$, $n = 30$, $r^2 = .92$). The ratio of ray length/ray weight indicates that at the Bay of LA ($\hat{y} = 0.6386 x + 5.4727$, $n = 30$, $r^2 = .86$) smaller (ray weight) specimens had longer ray lengths that differed significantly (ANCOVA, $p<0.5$) from the population at Loreto ($\hat{y} = 0.7722 x + 4.8259$, $n = 30$, $r^2 = .92$) where the larger (ray weight) specimens were found with the longer ray lengths.

Figure 8: Allometric plot of Pyloric Caeca in grams (Y) versus Total Wet Weight in grams (X) for both locations.


Loreto
Bay of LA
Pyloric Caeca (g)
Total Weight (g)
0
1
2
3
5
15
25
35
45
55

A comparison of the ratio of ray weight/gonad weight indicates that there is no significant difference in the slopes of the populations at Loreto and Bay of LA with a combined regression ($\hat{y}$ = 7.3131x10^{-2} x + -0.1198, n = 60, r^2= .60).

Eating Observations:

At Loreto, there was a significantly greater (Z=3.4) proportion (147/245) of individuals eating at depths >4.5 meters than at the shallower depths (50/121, Figure 9). In contrast, at the Bay of LA the proportion (19/36) of individuals eating at depths >4.5 meters was not significantly different (Z=1.08) from those at shallower depths (21/32, Figure 9). Both populations (shallow and deep) at the Bay of LA had proportions of individuals eating that were similar to the deep population at Loreto.

Activity Rate:

Comparison of activity rates indicate that both locations show the same general trend through the 13°C to 27°C range, although each location had significantly ($p<.05$, Anova and Scheffe's Test) different rates at 31°C (Figure 10).

Figure 9: A comparison of the proportions of individuals eating (shallow and deep) at both locations.

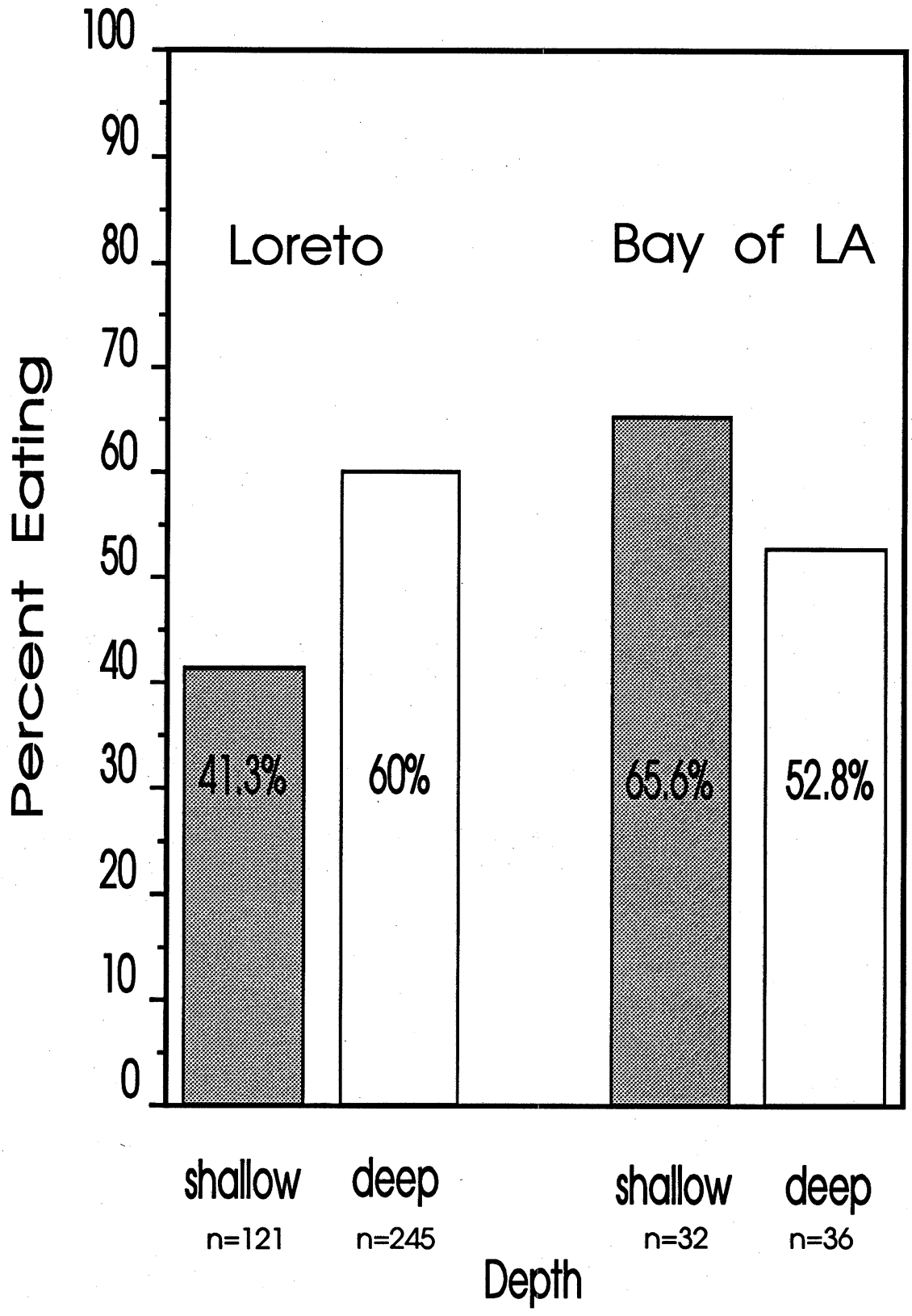
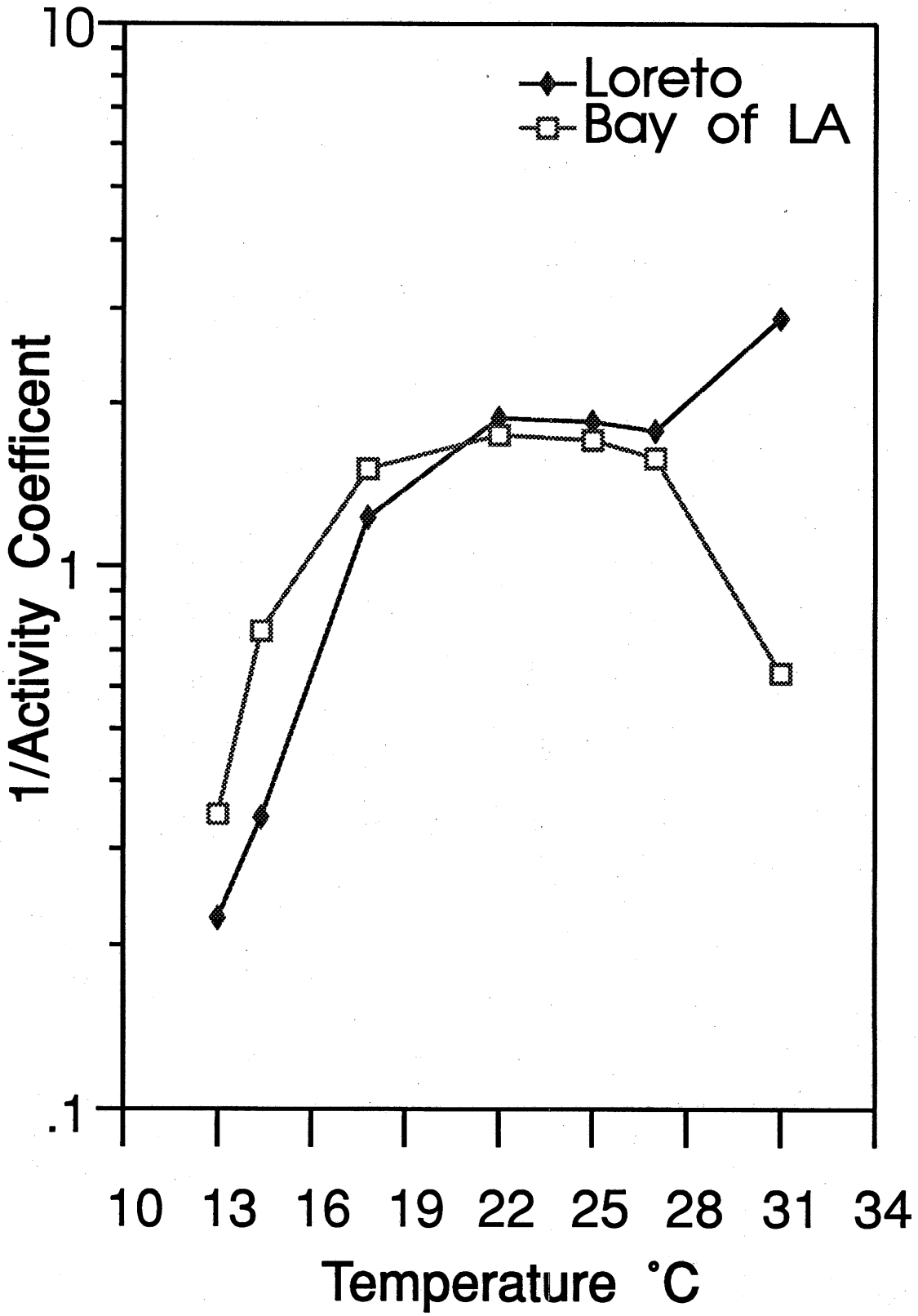

100
90
80
70
60
50
40
30
20
10
0
Percent Eating
Loreto
Bay of LA
41.3%
60%
65.6%
52.8%
shallow
deep
shallow
deep
n=121
n=245
n=32
n=36
Depth

Figure 10: A comparison of activity rates between specimens found at Loreto and the Bay of LA.


10
1
.1
Loreto
Bay of LA
1/Activity Coefficent
10 13 16 19 22 25 28 31 34
Temperature °C

The temperatures of 14.4°C and 17.8°C represent the wintertime lows for the Bay of LA and Loreto respectively. At Loreto, differences in rates between the temperatures of 14.4°C and 17.8°C were significant ($p<.05$, Anova and Scheffe's Test). At the northern location (Bay of LA), although the trend was also observed, there was no significant difference in activity rates between temperatures of 14.4°C and 17.8°C. Activity rates of the Bay of LA specimens at lower temperatures were slightly but not significantly elevated compared to Loreto. It should also be noted larger specimens generally took longer to right themselves than did smaller specimens at the same temperature.

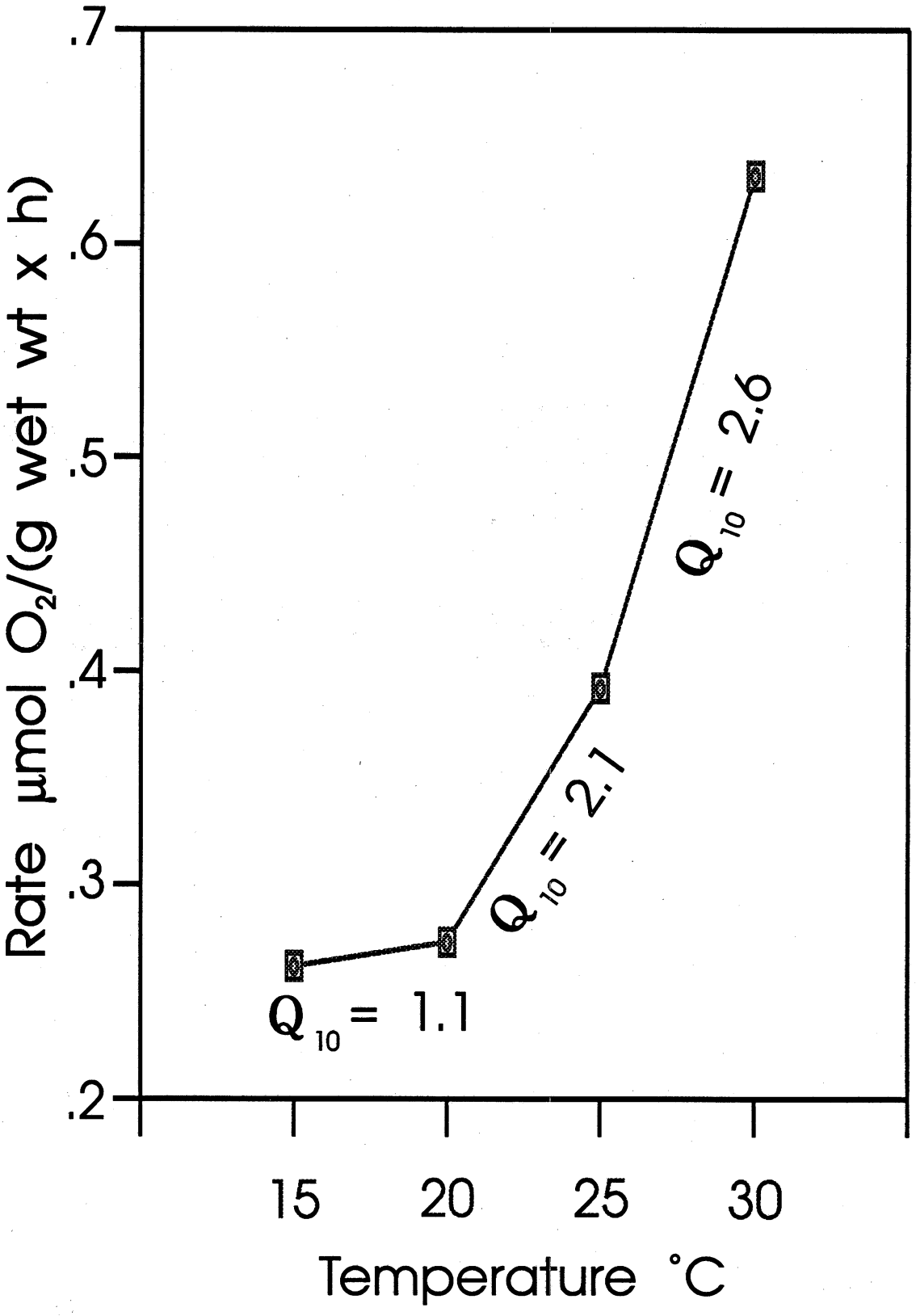
Rates of Oxygen Consumption:

The respiration rate for Phataria unifascialis appears to increase with increase in water temperatures (Figure 11). Q_{10} is a value which represents a proportional increase in respiration rate associated with a 10°C increase in temperature (Schmidt-Nielsen 1990). The Q_{10}'s for normal physiological measurements usually fall within the range of 2 to 3. The calculated Q_{10}'s for P. unifascialis were in the range of 2 to 3 except at the lowest temperatures where the respiration rate was higher than expected (Figure 12).

Figure 11: Respiration rates for Phataria unifascialis over the thermal range of 15 to 30°C.

Respiration Rate
μ mol O2/(g wet wt x h)
15°C
20°C
25°C
30°C
1.0
.9
.8
.7
.6
.5
.4
.3
.2
.1
0
0 to 10
10 to 20
20 to 30
30 to 40
40 to 50
50 to 60
60 to 70
70 to 80
80 to 90
90 to 100
100 to 110
110 to 120
120 to 130
130 to 140
140 to 150
150 to 160
mm Hg

Figure 12: The Q_{10}'s for Phataria unifascialis over the thermal range of 15 to 30°C. Values calculated at pO_2 of 100-110 mm Hg.


.7
.6
.5
.4
.3
.2
Rate µmol O_2/(g wet wt x h)
Q_{10} = 1.1
Q_{10} = 2.1
Q_{10} = 2.6
15
20
25
30
Temperature °C

DISCUSSION

At the Bay of LA, some factor must be responsible for the reduced overall abundance and absence of smaller size classes of *P. unifascialis*. Predation on adults does not appear to be a factor since specimens were never found with evidence of damage. Although the species is parasitized by the mollusc *Thica callista* (Kerstitch 1989, Dushane 1984) no studies exist that suggest this parasitism has any marked impact on *P. unifascialis*' population size or reproductive potential. Even if *Thica* does impact on *P. unifascialis*, this would not explain their reduced abundance at the Bay of LA, since the range of this mollusc does not extend that far north (Kerstitch 1989).

Since water temperature at the Bay of LA averages 3°C cooler year round compared to Loreto, reduced temperatures may alter reproductive cycles or growth rates of *P. unifascialis*, resulting in lower population density. Reproductive cycles can also be influenced by variations in latitude (Pearse 1968). Changes in size of gonads, usually indicated by gonadal index (Boolootian 1966, Lawrence and Lane 1982) can often be used to indicate such cycles. This study shows that during spring, even though the water temperature at the northern location (Bay of LA) is 3°C cooler and the location is 3° farther north in latitude, *P. unifascialis* at both locations are producing equivalent

amounts of gonad tissue. This suggests variations in temperature and latitude are not sufficiently different between the two locations to affect the total amount of gonad production in mature individuals *per se*, so it is unlikely differences in populations arise directly from this factor. Although gonad production is similar for specimens of the same size from both locations, behavioral differences appear to exist between potentially reproductive adults from the two locations. At the southern location (Loreto), larger specimens with significantly greater amounts of gonad tissue are segregated into a distinct population in the shallow depths (<4.5 meters), while smaller specimens with less gonad tissue were found grazing at greater depths (>4.5 meters). By comparison, at the northern location (Bay of LA) no such segregation was evident, and specimens from all depths had similar amounts of gonad tissue and were grazing in similar proportions as the non-reproductive population at Loreto. In addition, there appears to be a trend suggesting that a larger body size is required before individuals become sexually mature at the Bay of LA, but due to this location's small sample size this conclusion is uncertain.

My visual observations suggest this species has its greatest amount of gonad tissue during autumn and it is probably this season when gametes are shed. If my visual observations are accurate, larvae would be exposed to the coolest temperatures of the year shortly after

fertilization. Although cooler water temperatures of the northern location (Bay of LA) don't appear to inhibit gonad production in mature adults, these temperatures might affect gametes and/or larvae.

Recruitment is usually defined as the appearance of individuals that can be easily found (Ebert 1983). In this study, no specimens smaller than 4 cm were ever found at either location. It is possible smaller individuals might have been found if collection methods had included turning over rocks. Before larvae could be found, studies need to be performed that identify larva of P. unifascialis and the time when this species sheds gametes. Rowley (1989) showed newly metamorphosed echinoids can be found and that considerable mortality occurs before they reach the size at which they would otherwise be considered recruits. Barnes (1987) indicates that in most asteroids, liberated eggs and individuals in later developmental stages are planktonic. Although I did not observe larvae or determine the length or mortality levels of the larval stage of P. unifascialis, the high mortality rate identified in metamorphosed planktonic echinoids is probably similar for other echinoderms whose gametes and larvae are planktonic. It is possible P. unifascialis broods its eggs, although this seems unlikely since most brooders are located in polar regions (Barnes 1987). However, further studies are need to test the possibility of this species' being a brooder.

Thorson (1950) considered the major influence of temperature was to delay or advance development of invertebrate larvae, thereby increasing or decreasing exposure to predators. McEdward (1985) supports Thorson's idea with echinoderms, showing that echinoplutei have higher rates of growth, development, and metabolism at higher temperatures. Although larvae were not examined in this study, it would be reasonable to assume higher water temperatures at the southern location (Loreto) are likely to enhance the rate of development of larvae in this region. Lower temperatures at the Bay of LA, on the other hand, may extend the time required for larval development (Thorson 1950). Further studies need to be done to evaluate this idea. Ultimately, whether or not the influence of temperature results in increased predation pressure on larvae at the Bay of LA has yet to be determined. This idea deserves further investigation since it provides a reasonable alternative explanation for the reduced abundance observed at this location.

The influence of temperature is a very appealing explanation for the reduced abundance of P. unifascialis observed at the Bay of LA; however, McClintock (1988) found low levels of larval and juvenile recruitment for some asteroids may be related to other aspects of life-history such as food availability. Thorson (1950) also emphasized the importance of food abundance and its influence on the

growth of marine invertebrate larvae. Hart and Scheibling (1988) concluded that food abundance does affect the growth of echinus rudiment, but these effects are smaller than effects of temperature.

In considering effects of food availability on adult echinoderms, Lawrence (1985) suggested that individual size and population biomass is a function of food availability. Animals in superior nutritional condition will exhibit a higher pyloric caeca index (McClintock 1988). A comparison of pyloric cecal indices of the northern location (Bay of LA) and the southern location (Loreto) should serve as an indicator of significant differences in food supply. Population differences in gonadal and pyloric cecal development have been attributed to differences in food supply in the sea stars Asterias rubens (Vevers 1949, Barker and Nichols 1983), Pisater ochraceus (Mauzey 1966), Patiria regularis (Crump 1971), and Odontaster validus (Pearse 1965). This study shows that populations at each location (Bay of LA & Loreto) had different quantities of pyloric caeca. These differences, however, seem to be the result of the influence of a smaller sub-adult (individuals with significantly less gonad tissue) deep population at Loreto, since comparison of similar sized specimens from both locations indicates comparable quantities of pyloric caeca.

It is unlikely, therefore, that the northern population is limited by food availability.

Regression analysis suggests that as P. unifascialis increases in total weight, specimens from Loreto grow proportionally longer rays and have larger amounts of pyloric caeca (see Figure 11) than those the Bay of LA. Increased food quantity and quality have been shown to result in higher growth rate and larger body size in sea stars (Lawrence and Lane 1982). Although growth rates were not directly measured in this study, results of these regressions suggest relationships might exist between the ratio of pyloric caeca/total weight, ray length/total weight, and growth rate. The higher ratios actually observed at the southern location (Loreto) do not appear to be the result of different levels of food availability since specimens of comparable size from both locations have similar pyloric caecal indices; however, one would expect metabolism of poikilotherms to be increased at higher temperatures. The population from the northern location (Bay of LA) might best be described as less robust since specimens are capable of developing into larger size classes, but doing so with a smaller proportion of pyloric caeca/total weight. Further studies should include a lipid analysis of pyloric caeca from both locations to determine whether a population from one location was quantitatively in a superior nutritional condition (McClintock 1988).

Although Lawrence and Lane (1982) have coupled high growth rate and larger body size, this study suggests larger body size does not necessarily reflect higher growth rates since the largest specimens were found at the northern location (Bay of LA), while the specimens from the southern location (Loreto) with greater proportions of pyloric caeca and relatively longer ray lengths would be assumed to have higher growth rates. As previously stated, though growth rates were not directly measured, one observation should be noted. Upon completion of the dissection, specimens with one ray removed were returned to their natural habitat in sites that could be identified later. Prior to the transplant, the Loreto site had relatively few specimens, while the Bay of LA site had no specimens. A survey of those sites one year later showed that, at the Bay of LA, one third of the dissected specimens could still be identified by a ray that was only one fifth the length of the others. By comparison, at the Loreto site, all specimens found appeared to have ray lengths of equal size. Whether these observations are the results of different rates of growth and regeneration at each location or due to other factors such as predation or migration is not known.

McClintock (1988) emphasizes the importance of using biomass and not body size alone as an indicator of food availability. While on the average, smaller specimens were found at the southern location (Loreto), the total biomass

per unit area was still much higher as evidenced by transect results. A greater total biomass with smaller individuals would be expected in a area where optimal conditions are capable of producing a greater number of recruits that must then compete for the available food. It appears that both locations have an adequate food supply; therefore this factor alone would not limit the distribution of P. unifascialis. Reasons for this conclusion will vary with each location. At the northern location (Bay of LA), food supply is sufficient so individuals are capable of obtaining large sizes, whereas at the southern location (Loreto), observed population densities and apparent higher growth rates could not be supported without an adequate food supply.

Although the eating observations cannot determine feeding rates, they can help characterize the populations studied. Juvenile asteroids have feeding rates much higher than adults of the same species (Hancock 1955, Feder & Christensen 1966, Feder 1970). The deep population at Loreto appears clearly to be a sub-adult population, as evidenced by smaller sizes, reduced amounts of gonad tissue, and a higher proportion of individuals found eating. Populations (both shallow and deep) at the northern location (Bay of LA) appear to behave like the deep population at Loreto by having similar proportions of individuals eating.

Thus, although they are potentially reproductive adults, at least during the time of this study they appeared to be acting like juveniles rather than adults.

Activity rates of specimens from both locations indicate there is a range of temperatures (22-27°C) at which activity stays essentially the same (see Figure 10). It should be noted this range excluded the extreme temperatures. Specimens from both locations show the same general trend, but the Loreto sample shows activity rates that are reduced at the lower temperatures as compared to the Bay of LA sample. One possible explanation is acclimation. The Loreto specimens were maintained in water temperatures of ≈24°C, whereas temperature at the Bay of LA at the time of this experiment was 16°C. The Loreto specimens might have experienced some form of stress at 13°C while being subjected to temperatures that were cooler than the temperature to which they were acclimatized by at least 11°C, while the Bay of LA specimens possibly experienced stress at 31°C, a temperature 15°C warmer than their acclimatized temperature. Also, during the period when Loreto specimens were being maintained in the laboratory, electricity on one occasion was accidentally shut off overnight, resulting in specimens being temporarily subjected to temperatures as low as 9°C. At this temperature, individuals appeared limp with ambulacral grooves closed and overturned specimens made no apparent

effort to right themselves. When water temperature was returned to the normal range, specimens became firm again, reopened their ambulacral grooves and extended their tube feet. The appearance just described was also observed with the Bay of LA specimens at the 31°C temperature. Another plausible explanation is that, at the Bay of LA, there might be some type of populational difference allowing for elevated activity rates in the Bay of LA specimens at the lower temperatures, while greatly reducing rates at the highest temperatures; that is, this population might be adapted to functioning at cooler temperatures. The high temperatures of this experiment are outside the normal thermal range for the Bay of LA, so it would not be genetically advantageous for the species to develop or maintain allozymes that are efficient at those temperatures, since they would not normally be encountered. A study comparing allozymes from both locations could be done to see if any speciation might be occurring. A third possibility for this difference might be the Loreto specimens were measured while in an aquarium system with perhaps a reduced food supply, whereas Bay of LA specimens had an abundant food supply while being measured in the field (Sloan 1980). Further studies are needed to determine whether the anomalies in activity rates are the result of temperature acclimation or of an inadequate food supply.

The Q_{10}'s calculated from respiration rates seem to indicate that as P. unifascialis nears the coolest temperature, its metabolic rate begins to level off. This response appears to begin prior to being subjected to the most extreme temperatures. Respiration rates had the greatest acceleration in the range of 25°C to 30°C which produced a Q_{10} of 2.6 (see Figure 12). Such a value suggests the species is most sensitive to temperature changes over this range. In addition, at each temperature, respiration rates decline as the partial pressure of O_2 drops, but there appears to be a range of low partial pressures where respiration rates increase, possibly the result of trying to escape or adjust to anoxic conditions (see Figure 11). These results, along with results of the activity rates suggest there is an optimum temperature range of inhabitancy for this species. Golikov and Scarlato (1973) suggest a method for indirectly defining the optimum temperatures of inhabitancy for cold-blooded animals in the northern hemisphere. This optimum range should fall between the wintertime low for the southern location and the summertime high for the northern location (see Figure 4). By applying Golikov and Scarlato's method to temperature ranges of the locations in this study, it appears an optimal temperature range of ≈18 to 28°C exists for seven months (May to November) at the Bay of LA, and 9 months (November to July) at Loreto. Although both locations have periods of time

outside the optimum temperature range, an important difference between these sub-optimal periods bears special recognition. Metabolic rates are at their lowest during the sub-optimal temperature period (December to April) at the Bay of LA. By comparison, Loreto's sub-optimal temperature period (August to October) represents a time when metabolic rates are highest. It seems reasonable to suggest a correlation exists between the optimal temperature range of inhabitancy and the range of temperatures where respiration rates show the greatest increase while activity rates are stabilized. All three of these factors can be used to identify an optimum range of temperatures. Such a range could be used to explain the observed conditions at the Bay of LA, since metabolic processes are reduced at the lower temperatures. It is possible the smaller time period of optimum temperatures would reduce the reproductive success of the species at this location. Further studies need to be conducted in order to confirm or reject this idea.

In summary, several lines of evidence suggest Phataria unifascialis at the Bay of LA is a peripheral population and may not be successfully reproducing annually. First, there was a lower population density. Second, the Bay of LA population was depauperate in the smaller size classes. Third, there was no distinct reproducing sub-population. And last, laboratory observations in temperature sensitivity suggest that the lower temperatures of the Bay of LA may be in part directly responsible for the lower success there.

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